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Parental provisioning in relation to offspring sex and sex ratio in the great tit (*Parus major*)

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Summary

Sex-biased parental care is expected if the offspring sexes differ in their energetic needs or if they differentially affect their parents' reproductive success after independence. Furthermore, parents should adjust provisioning rate and prey size to the needs of individual nestlings and the entire brood. We investigated experimentally whether parental care in the great tit varied with individual offspring sex and brood sex ratio. We created broods of skewed sex ratio and monitored parental provisioning behaviour as number and size of prey items brought to individual young and broods. We found that male and female nestlings were fed at equal rates and with equally sized prey items independently of the brood sex ratio. The male share of provisioning did not change with offspring sex or sex ratio. However, parents brought significantly larger prey items to male biased broods with a small decline in provisioning rate such that the total amount of food brought did not change. Our findings suggest that parents did respond to manipulated brood sex ratio without distinguishing between the individual nestling sexes. Bringing larger prey items at slightly lower rates to male biased broods might reduce the cost of solicitation activities or satisfy increased needs in those broods.

Keywords: parental care, parental food allocation, *Parus major*, sex-biased provisioning, sex ratio manipulation.

Introduction

In order to maximise their fitness, parents should trade-off the costs of producing and raising a certain sex to independence against the potential fitness

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benefits they can expect from investing in this offspring sex (Fisher, 1930; Trivers & Willard, 1973; Charnov, 1982; Frank, 1990). Several variables like laying date (Dijkstra et al., 1990; Daan et al., 1996; Laaksonen et al., 2004b), parental condition (Kölliker et al., 1999; Nager et al., 1999; Whittingham & Dunn, 2000), male attractiveness (Ellegren et al., 1996; Sheldon et al., 1999), territory quality (Komdeur, 1998), food availability (Appleby et al., 1997), pair bond duration (Green, 2002) or relative position in the laying sequence (Bednarz & Hayden, 1991; Badyaev et al., 2002) have already been described as potential factors affecting the relative fitness returns of male and female offspring in birds. Additionally, different energetic requirements of the two offspring sexes might cause differential parental investment in sons and daughters and, thus, be a reason for adaptive sex allocation (Fisher, 1930; Charnov, 1982).

In avian species where the young strongly depend on parental care, differential provisioning of food towards the two offspring sexes is one mode of sex allocation (Charnov, 1982). Furthermore, parents can adjust their provisioning behaviour to reduce negative consequences of competitive interactions among nestlings thereby minimizing nestling control over food allocation (Kölliker et al., 1998; Tanner et al., 2007). Indeed sex-biased parental care has been shown to occur in a range of bird species where either one or both parents preferentially provision one offspring sex (Stamps, 1990; Gowaty & Droge, 1991). Even in species with little or no sexual size dimorphism of nestlings we can expect differential parental provisioning of the offspring sexes as there is evidence that the sexes differ in their competitive abilities or physiological requirements (Boncoraglio et al., 2008; Nicolaus et al., 2009). Additionally, parents of the different sexes might have different optimal investment strategies towards sons and daughters which could lead to a conflict over parental care (Gowaty & Droge, 1991; Lessells, 2002).

Descriptive studies on parental provisioning in relation to offspring sex and sex ratio have so far provided mixed results. Several studies on pre-fledging parental care found an increased provisioning rate of either one or both parents to sons or male biased broods (Yasukawa et al., 1990; Westneat et al., 1995; Nishiumi et al., 1996; Westerdahl et al., 2000; Green, 2002; Magrath et al., 2004). Others found increased parental effort to daughters or female biased broods (Stamps et al., 1987; Gowaty & Droge, 1991) and yet others found no relation between offspring sex or brood sex ratio and parental provisioning behaviour (Leonard et al., 1994; Whittingham et al., 2003).

Drawing conclusions from those results is rather difficult because parental provisioning behaviour and primary sex ratio might both be associated with environmental variables or parental traits that were not experimentally controlled. To circumvent this problem experimental manipulations of brood sex ratio have been performed to investigate sex-biased provisioning and to determine if parents adjust their provisioning behaviour in a predictable manner (Fiala, 1981; Røskft & Slagsvold, 1985; Leonard et al., 1994; Lessells et al., 1998; Green, 2002; Laaksonen et al., 2004a; Magrath et al., 2007). Interestingly, most of these studies failed to find an effect of brood sex ratio on parental provisioning behaviour (but see Green, 2002; Magrath et al., 2007) even in a species where the larger offspring sex has been shown to have higher energetic requirements (Fiala, 1981). In most of these studies brood sex ratio manipulations typically consisted of only unisex broods (Fiala, 1981; Røskft & Slagsvold, 1985; Green, 2002; Magrath et al., 2007) although some had equal sex ratio controls (Lessells et al., 1998; Laaksonen et al., 2004a). Therefore, they might not only have lacked within-brood stimuli for sex-discrimination by parents (Lessells et al., 1998) but also missed the opportunity to investigate whether parental provisioning to nestlings of different sexes within the nest is related to brood sex ratio and/or parental sex (but see Leonard et al., 1994).

In this study, we aimed at providing more insight into whether parents provision the two offspring sexes differently and how they change their provisioning behaviour towards broods and towards individual nestling sexes in response to changes in brood sex ratio in the great tit (*Parus major*). Studies on parental investment in relation to brood sex ratio in the great tit so far provided mixed evidence (Lessells et al., 1998; Radford & Blakey, 2000). A correlative study by Radford & Blakey (2000) showed stronger paternal nest defence when there were more male nestlings in the broods, but Lessells (1998) found no effect of experimental brood sex ratio on parental provisioning behaviour (feeding rate, prey size, visit duration, proportion of male visits) or nest defence.

We created broods of known sex ratio and subsequently monitored parental provisioning behaviour to individually marked young by means of video observation in the nest box. As measures of parental provisioning behaviour we used provisioning rate and average prey size fed to broods and to individual nestlings within a brood. Additionally we examined the proportion of provisioning visits to broods and nestlings performed by the male.

This should allow us to detect a specific response by only one parent that is compensated for by the other.

Already at the age of 10–14 days, male great tit nestlings are significantly heavier and have larger tarsi than female nestlings (Nicolaus et al., 2009; weight difference 4–8%; difference in tarsus length 2–6%; Oddie, 2000). Therefore, we might expect male young to need more energy and, thus, receive more food as would male biased broods. Furthermore, it has been shown previously that gape size differences between nestlings (potentially also between the nestling sexes) may result in constraints on prey sizes fed to smaller and larger individuals (Slagsvold & Wiebe, 2007). Additionally, under stressful conditions male nestlings have been shown to be better competitors compared to their females nest mates (Oddie, 2000; Nicolaus et al., 2009). We would, therefore, expect that female nestlings in male biased broods receive less food compared to females in female biased broods.

Methods

Study population and experimental design

The study was conducted between April and July 2004 in a great tit population breeding in the Lauwersmeer area, which is situated in the northeast of the Netherlands (50°23'N, 6°14'E). Four nest box areas of about 9 ha each were newly established in early March 2004. Each plot consisted of 50 nest boxes in a regular 50 m grid. The woodlots were deciduous forests (about 30 year old plantations of mainly oak (*Quercus*), poplar (*Populus*), birch (*Betula*) and elder (*Alnus*) and were separated by at least 700 m of open grassland or forest patches without boxes. This study was part of a long-term project aiming at manipulating the fledgling sex ratio on a plot level (sex ratio is defined as the proportion of males). For this purpose two plots were randomly assigned to contain male biased first broods (plots 1 and 3, average brood sex ratio after manipulation \pm SD: 0.77 ± 0.11 , $N = 22$) and two plots to contain female biased first broods (plots 2 and 4, average brood sex ratio after manipulation \pm SD: 0.27 ± 0.19 , $N = 25$). First broods were defined as all broods that started less than 30 days after the start of the very first brood in that year, excluding replacement broods of known females.

Nests were visited at least once a week to estimate the date the first egg was laid (assuming one egg was laid each day), clutch size and presumed

start of incubation. From day 12 after the onset of incubation nests were checked daily to determine hatching date of the first young in each nest (day 0). On day 2 all nestlings of a brood were individually marked by clipping the ends of their toe nails using an individual combination (St. Louis et al., 1989) and a small blood sample (about 5–10 μ l) was taken from the tarsal vein. Blood was stored in 100% ethanol and was transported to the lab for immediate molecular sexing.

On day 6 after hatching, the brood sex ratio of in total 37 first broods was manipulated by cross-fostering nestlings between broods of matching hatch date between plots. Brood sex ratios within plots were biased to contain primarily offspring of the sex corresponding to the plot treatment; thus, we aimed at a brood sex ratio of 75% male young in male-biased plots and 25% male young in female biased plots. We always kept at least one nestling of the opposite sex in the nest because parents might need both sexes to be present for discrimination between the sexes (Lessells et al., 1998). Variation in the degree of experimental brood sex ratio within plots arose because of variation in brood size and because broods with matching hatching dates sometimes did contain too many or not enough young of the necessary sex for swapping. Within plots, brood sex ratios after manipulation, thus, showed variation ranging from 55 to 90% in male biased plots and from 9 to 45% in female biased plots. This is in the range of natural sex ratios of first and second broods in the study year (0–90%, $N = 86$, also including broods from non-experimental plots). The brood sex ratio before and after manipulation were not correlated, neither between plots (all manipulated broods: $r_s = 0.052$, $N = 37$, $p = 0.761$; broods in provisioning analysis: $r_s = -0.38$, $N = 21$, $p = 0.088$) nor within plots (all manipulated broods: plot 1: $r_s = -0.02$, $N = 11$, $p = 0.957$; plot 2: $r_s = -0.118$, $N = 9$, $p = 0.763$; plot 3: $r_s = 0.119$, $N = 8$, $p = 0.779$; plot 4: $r_s = 0.561$, $N = 9$, $p = 0.116$). Brood size was accidentally altered for two broods (± 1 nestling) but else remained unchanged. All experimental broods contained both foster young and own young that had not been transferred.

Molecular sexing

DNA was extracted using the Chelex methods described by Walsh et al. (1991). Sex of the young was determined following Griffiths et al. (1998).

The PCR products were separated by electrophoresis on a 2% agarose gel. Of the 1478 nestlings that were sexed in 2004 (including birds from nearby unmanipulated areas), 172 (11.6%) were seen as adults during winter nest box checks or as breeders during the next breeding season and phenotypic adult sex in all cases agreed with the result of the molecular sexing. For only one nestling that survived to fledging, we could not clearly identify the sex. This individual was excluded from further analysis.

Assessment of parental care

We chose to measure parental care four days after the manipulation had taken place to give birds the possibility to get used to the new brood composition but also because parents are less likely to leave the brood when disturbed. On day 9 an empty camera box was fitted on top of the nest box to habituate birds to the setup.

On day 10 a camera (SONY video Hi8 handycam with a NP-F750 battery) was fitted in the camera box. Additionally, nestlings were individually marked on the head with non-toxic, red acrylic paint (Van Gogh, Royal Talens, Apeldoorn, The Netherlands), which was well visible using infrared recording mode. The marking was performed by using an imaginary three by three grid on the head with a spot at one of nine possible positions to recognize all nestlings individually. When more than nine nestlings were present a combination of two spots was used. After letting the parents get used to the camera setup for one hour, a 3-h recording was started. The camera used (infrared) night vision because of lack of light in the nest box. Recordings were done during daytime, between 0900 and 1200 h and between 1400 and 1700 h.

All tapes were assigned random numbers to allow blind analysis of provisioning observations. All observations were done by the same person. The first 30 min of each tape were not analysed to standardize the time parents needed to return to feed the nestlings after onset of the tape.

In total we managed to obtain video recordings of 21 experimental broods (plot 1: $N = 6$; plot 2: $N = 7$; plot 3: $N = 2$; plot 4: $N = 6$). We excluded individual observations of visits where we could not identify the parental sex ($N = 1$). This left a sample size of 2958 provisioning events on which the analysis of per brood provisioning behaviour was based. For the per nestling analysis of provisioning behaviour we additionally excluded

visits where markings of the fed nestling were not clearly visible (12% of all observations, no difference between visits of male and female parent: paired t -test; $t \leq -0.01$, $df = 20$, $p = 0.996$). This left in total 2609 provisioning events to 194 young.

The following relevant parameters were scored during each feeding visit on the video recording: sex of the parent (females have a duller black head but ring combinations were also used for identification), identity of the nestling fed and size of the prey delivered. Latter was scored using the size of the parental beak as reference (Kölliker et al., 1998; Lessells et al., 1998; Naef-Daenzer et al., 2000) where an item that had the same volume as the parental beak received a value of 1; scores of prey sizes ranged from 0.5 to 3.5.

Statistical analyses

Since the experimental setup had a hierarchical structure (nestlings are nested within broods within plots) we used generalized linear mixed models (MLwiN 2.0, Rasbash et al., 2004) to adequately analyse the relationship between provisioning behaviour towards individual nestlings within a brood and towards broods within plots and the variables of interest. Therefore, plot, brood and individual nestling were modelled as random effects (levels) for the analyses on individual nestlings. For other analyses Statistica version 7 (StatSoft, 2004) was used.

As a fair amount of provisioning visits was delivered to nestlings that could not be identified we chose to perform not only an analysis on individual nestlings but also on entire broods where plot and brood were used as random effects. Any differences between those two sets of analyses might reveal a bias in the sample of 'unidentifiable' nestlings. To investigate different aspects of provisioning behaviour we looked at three different dependent variables, which were (1) provisioning rate (total number of provisioning visits to a nest per hour), (2) average prey size delivered to a brood and (3) 'relative male provisioning' as the proportion of provisioning visits done by the male parent. As provisioning rate and average prey size to broods tended to be positively correlated ($r = 0.40$, $N = 21$, $p = 0.07$, Figure 1), a multivariate normal response model was used in order to account for the effect of covariance between those two response variables. As we expected the relative feeding rate fed to nestlings and broods to remain constant rather than

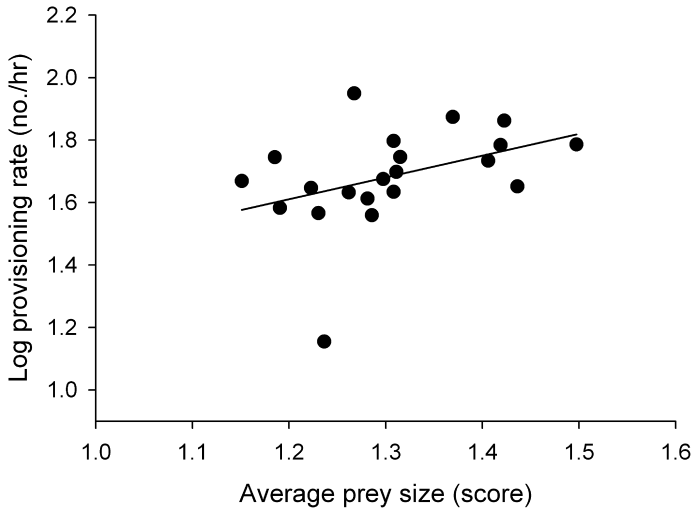


Figure 1. Correlation between provisioning rate (log transformed) and average prey size fed to broods of great tits. The regression line is based on raw data.

the arithmetic differences in feeding rates we log transformed provisioning rate (unless stated otherwise). For provisioning rate and prey size z -scores ($z = (\chi - \mu)/\sigma$) were used and analysed in a normal response model. Additionally, we created a composite measure for ‘amount of food provided per hour’ by simply multiplying the average prey size and provisioning rate, we log-transformed it and analysed it using a normal response model. For ‘relative male provisioning’ a binominal response model with an logit link was employed using total number of feedings per hour as the offset.

Because broods within plots were manipulated in the same direction as the plot treatment, we analysed the effect of variation in experimental brood sex ratio within plots as well as the effect of the plot sex ratio treatment. Therefore, the experimental brood sex ratio was expressed as the deviance of final experimental brood to final experimental plot sex ratio (at day 6) at the brood level (referred to as relative experimental brood sex ratio). The plot sex ratio treatment was expressed as a categorical variable (with female biased as reference) at the plot level. A similar approach was used to investigate original brood and plot sex ratio with the deviance of original brood to original plot sex ratio (at day 6) on brood level (referred to as relative original brood sex ratio) and original plot sex ratio on plot level. Relative original and experimental brood sex ratio were not correlated ($r_s = -0.14$, $N = 21$, $p =$

0.53). Furthermore, we tested the effect of time of day, laying date and brood size at day 10 on provisioning rate, prey size and relative male provisioning. We centred all continuous explanatory variables on their total population averages.

For the second set of models, we fitted plot, brood and nestling as random effects. The same three dependent variables were analysed using the same kind of models as in the per brood analysis with the only difference that they were calculated per individual nestling. In a similarly way we analysed variation in the total amount of food provided to individual nestlings per hour. As explanatory variables we tested sex of the nestling, whether it was an own or foster young, time of day, laying date, brood size at day 10, relative original brood sex ratio, original plot sex ratio, relative experimental brood sex ratio and plot sex ratio treatment category.

Each model originated from backward selection of possible explanatory variables and their interaction terms. Wald test was applied to determine the significance of explanatory variables as each term was removed from the model. Final models included the constant together with any statistically significant explanatory variable. Furthermore, non-significant terms were not included in the model summary tables unless they were of specific interest. When the model residuals were checked for normality and outliers, one data point of the per nestling analysis of relative male provisioning showed a leverage value of 0.36 which is more than $(3(k + 1)/n)$ the recommended cut-off point for identifying influential cases (Stevens, 1992). We excluded this point from further analysis (final model shown in the Results section).

Results

The original sex ratio of the broods (one-sample *t*-test; $t_{36} = -0.39$, $p = 0.701$) or plots (one-sample *t*-test; $t_3 = 0.01$, $p = 0.989$) did not significantly deviate from parity (with an average original brood sex ratio \pm SD of 0.49 ± 0.15 and an average original plot sex ratio \pm SD of 0.50 ± 0.05). The sex ratio manipulation of broods resulted in a significant absolute change in brood sex ratio (one-sample *t*-test; $t_{36} = 10.47$, $p < 0.001$) with an average change \pm SD of 0.01 ± 0.35 (min = -0.80 , max = 0.55). The average sex ratio of all manipulated broods however, did not differ from the average orig-

inal brood sex ratio (paired t -test; $t_{36} = 0.21$, $p = 0.837$). Female and male biased plots significantly differed in final brood sex ratio at day 6 (Mann–Whitney U -test: $Z = 5.20$, $N_1 = 19$, $N_2 = 18$, $p < 0.001$). The variables ‘time of day’ and ‘own or foster young’ were never significant and these results are, therefore, not mentioned. We will first discuss the results from the analysis of the per brood patterns and then of the per nestling provisioning behaviour.

Parental behaviour towards broods

Both male and female parent visitation rates ($r_c = 0.27$, $N = 21$, $p = 0.231$) and average prey sizes ($r_c = -0.23$, $N = 21$, $p = 0.318$) brought to the same brood were not correlated. Male and female parents did not differ significantly in provisioning rate per hour (untransformed provisioning rate, mean \pm SE: male 27.99 ± 2.61 , female 23.16 ± 2.03 ; paired t -test: $t_{20} = 1.57$, $p = 0.132$) nor in the size of the delivered prey items (scored relative to parental beak size: male 1.30 ± 0.03 , female 1.28 ± 0.03 ; paired t -test: $t_{20} = -0.41$, $p = 0.685$).

The average prey size was significantly positively affected by the relative experimental brood sex ratio (Figure 2a) while the provisioning rate per hour declined only weakly with the brood sex ratio manipulation within plots (Figure 2b). Provisioning rate and average prey size fed to broods were related to the brood size at day 10 such that larger broods got significantly larger prey items and tended to receive food at a higher rate (Table 1, Figure 3). Additionally the original plot sex ratio was correlated with both provisioning rate and prey size: broods in plots that were originally more male biased received more feedings per hour and larger prey items than broods in plots that were originally more female biased (Table 1).

The analysis of the composite measure ‘amount of food provided per hour’ showed a significant positive correlation with brood size ($\beta \pm \text{SE} = 0.27 \pm 0.11$, $\chi^2_1 = 5.67$, $p = 0.017$) and the original plot sex ratio (Figure 4, $\beta \pm \text{SE} = 11.95 \pm 3.34$, $\chi^2_1 = 12.78$, $p < 0.001$). There was no variation on plot level and significant variation on brood level ($\chi^2_1 = 10.50$, $p = 0.001$). However, the ‘total amount of food provided per hour’ was not related to the plot sex ratio treatment ($\beta \pm \text{SE} = 0.33 \pm 0.32$, $\chi^2_1 = 1.05$, $p = 0.305$) nor to the relative experimental brood sex ratio ($\beta \pm \text{SE} = 0.12 \pm 1.30$, $\chi^2_1 =$

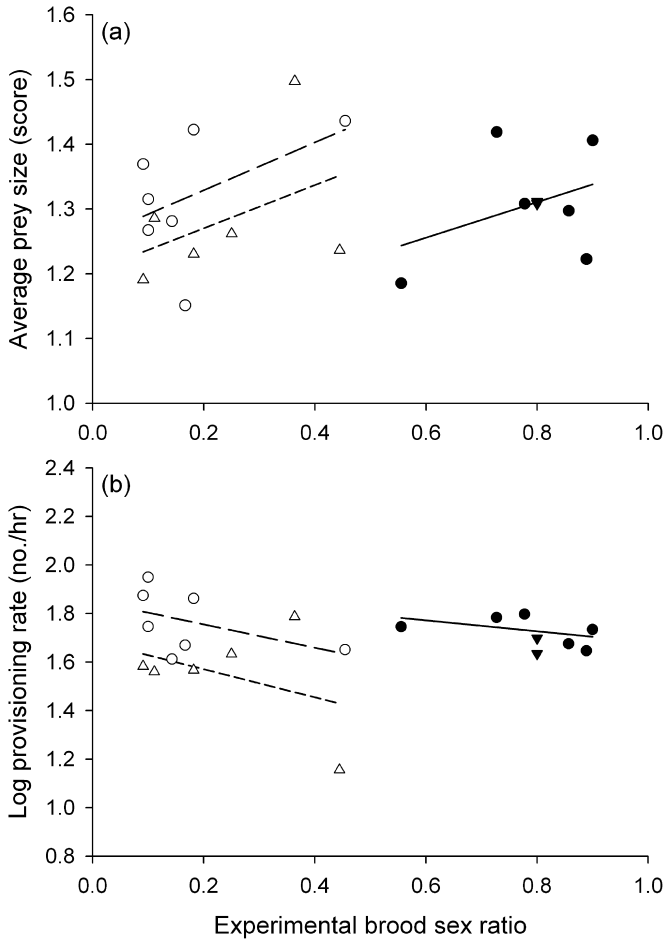


Figure 2. Effect of (relative) experimental brood sex ratio within plots on (a) the average prey size (relative to parental bill size) and (b) number of provisioning visits per hour (log transformed) in the great tit. Raw data are shown and regression lines and symbols refer to the four plots with two plot sex ratio treatments (plot 1, male biased = filled circles, solid line; plot 2, female biased = open circles, long-dashed line; plot 3, male biased = filled triangles down, no line; plot 4, female biased = open triangles up, short-dashed line).

0.01, $p = 0.925$) or the relative original brood sex ratio ($\beta \pm \text{SE} = -0.33 \pm 1.22$, $\chi^2_1 = 0.07$, $p = 0.787$).

The proportion of provisioning visits by the male parent to a brood was not affected by any sex ratio variable but significantly declined with laying date (Table 2).

Table 1. Mixed model summaries (log transformed) examining parental provisioning rate and average prey size to great tit broods ($N = 21$) in relation to the effect of plot sex ratio treatment, relative experimental brood sex ratio (deviance of experimental brood to plot sex ratio), original plot sex ratio, relative original brood sex ratio (deviance of original brood to plot sex ratio), brood size (at day 10) and laying date (date).

Explanatory variable	Provisioning rate				Average prey size			
	β (SE)	χ^2	df	p	β (SE)	χ^2	df	p
Final model								
Intercept	<-0.01 (0.19)	0.00	1	1.00	<0.01 (0.16)	0.00	1	1.000
Relative experimental brood sex ratio	–	–	–	–	3.69 (1.28)	8.27	1	0.004
Original plot sex ratio	11.29 (3.88)	8.47	1	0.004	7.46 (3.61)	4.27	1	0.039
Brood size	–	–	–	–	0.31 (0.11)	7.90	1	0.005
Rejected terms								
Plot sex ratio treatment	0.27 (0.33)	0.70	1	0.402	-0.39 (0.35)	1.20	1	0.274
Relative experimental brood sex ratio	-0.50 (1.56)	0.10	1	0.748	–	–	–	–
Relative original brood sex ratio	-0.75 (1.37)	0.30	1	0.586	2.11 (1.20)	3.06	1	0.080
Brood size	0.23 (0.12)	3.43	1	0.064	–	–	–	–
Date	-0.04 (0.07)	0.42	1	0.515	-0.04 (0.17)	0.35	1	0.554

Summaries are derived from the multivariate normal response mixed modelling procedure in MLwiN with plot and brood as random effects and where all non-significant variables were tested separately again in the final model. There was significant variation between broods for prey size ($\chi^2_1 = 10.50$, $p = 0.001$) and provisioning rate ($\chi^2_1 = 10.50$, $p = 0.001$) but no variation between plots. Provisioning rate and prey size showed some covariance on brood level ($\chi^2_1 = 1.85$, $p = 0.173$).

Parental behaviour towards individual nestlings

Provisioning rates by the male and female parent to an individual young were correlated ($r_c = 0.23$, $N = 194$, $p = 0.002$) but not the average prey sizes that the male and female parent fed ($r_c = 0.01$, $N = 194$, $p = 0.934$).

Male and female nestlings did not differ in provisioning visits received per hour (untransformed provisioning rate \pm SE, male young 4.81 ± 0.25 , female young 4.88 ± 0.22) nor in average prey size fed \pm SE (male young 1.33 ± 0.02 , female young 1.29 ± 0.01), independently of the brood sex ratio or plot sex ratio variables (Table 3). The relative experimental brood sex ratio had a significant positive effect on average prey size fed to an

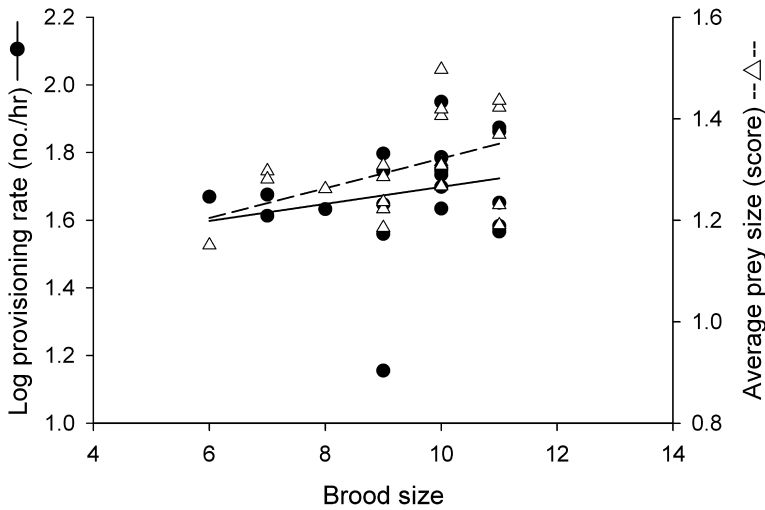


Figure 3. Relation between brood size at day 10 and provisioning rate (log transformed, filled circles, solid line) and average prey size (open triangles, dashed line) brought to broods of great tits. Regression lines are based on raw data.

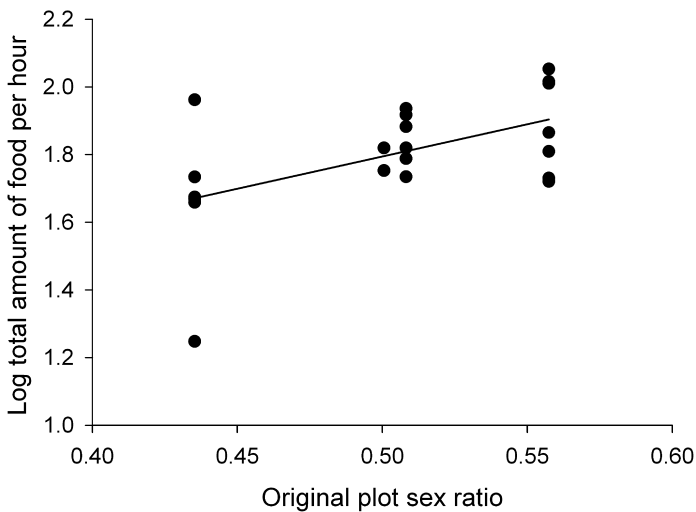


Figure 4. Correlation between original plot sex ratio (of the four study plots) and the total amount of food provided per hour (provisioning visits \times average prey size, log transformed) to great tit broods. The regression line is based on raw data.

Table 2. Model summaries examining relative male provisioning to great tit broods in relation to plot sex ratio treatment, relative experimental brood sex ratio (deviance of experimental brood to plot sex ratio), original plot and relative original brood sex ratio (deviance of original brood to plot sex ratio), brood size (day 10) and laying date (date).

Explanatory variable	β (SE)	χ^2	df	p
Final model				
Intercept	0.16 (0.13)	1.59	1	0.207
Date	−0.07 (0.02)	11.11	1	0.001
Rejected terms				
Plot sex ratio treatment	−0.02 (0.25)	0.01	1	0.920
Relative experimental brood sex ratio	0.39 (0.57)	0.49	1	0.485
Original plot sex ratio	−2.92 (2.18)	1.79	1	0.180
Relative original brood sex ratio	−0.01 (0.50)	0.001	1	0.977
Brood size	−0.04 (0.05)	0.82	1	0.364

Summaries derived from the binominal response modelling procedure in MLwiN where all non-significant variables were tested separately again in the final model. Plot and brood were kept as random effects in the model and showed some variation between plots ($\chi^2_1 = 1.019$, $p = 0.313$), $N = 21$.

individual young whereas there was no such effect on the provisioning rate (Table 3). In larger broods, individual nestlings received larger prey items than in smaller broods but they did not receive food more often (Table 3). Nestlings in plots that were originally more male biased received larger prey items and received food more often than nestlings in originally more female biased plots. Within plots, nestlings in broods that were originally relatively female biased received food at a higher rate (non-significant in per brood analysis but in the same direction). However, average prey size fed to nestlings showed no correlation with relative original brood sex ratio (Table 3).

The composite measure ‘amount of food provided per hour’ showed a significant correlation with original plot sex ratio (intercept, $\beta \pm \text{SE}$: -1.43 ± 0.33 , $\chi^2_1 = 20.98$, $p < 0.001$; original plot sex ratio, $\beta \pm \text{SE}$: 18.19 ± 6.98 , $\chi^2_1 = 6.80$, $p = 0.009$). There was no variation on plot level but significant variation between broods ($\chi^2_1 = 5.91$, $p = 0.015$) and nestlings ($\chi^2_1 = 86.17$, $p < 0.001$). There was no difference between the offspring sexes in the amount of food received per hour ($\beta \pm \text{SE} = -0.10 \pm 0.40$, $\chi^2_1 = 0.06$, $p = 0.008$; untransformed amount of food per hour $\pm \text{SE}$, male young

Table 3. Model summaries (log transformed) examining parental provisioning rate and average prey size to great tit broods in relation to nestling sex, plot sex ratio treatment, relative experimental brood sex ratio, original plot sex ratio, relative original brood sex ratio, brood size (day 10) and laying date (date).

Explanatory variable	Provisioning rate				Average prey size			
	β (SE)	χ^2	df	p	β (SE)	χ^2	df	p
Final model								
Intercept	0.01 (0.11)	0.004	1	0.949	0.01 (0.10)	0.01	1	0.933
Relative experimental brood sex ratio	–	–	–	–	2.19 (0.70)	6.05	1	0.014
Original plot sex ratio	6.16 (2.39)	6.62	1	0.010	4.58 (2.21)	4.32	1	0.038
Relative original brood sex ratio	–1.60 (0.73)	4.86	1	0.027	–	–	–	–
Brood size	–	–	–	–	0.24 (0.06)	14.76	1	<0.001
Rejected terms								
Sex	–0.10 (0.14)	0.48	1	0.487	0.05 (0.15)	0.09	1	0.758
Plot sex ratio treatment	0.11 (0.23)	0.21	1	0.646	–0.23 (0.21)	1.19	1	0.275
Relative experimental brood sex ratio	–0.18 (1.00)	0.03	1	0.854	–	–	–	–
Relative original brood sex ratio	–	–	–	–	0.13 (0.82)	0.03	1	0.872
Brood size	–0.08 (0.08)	0.95	1	0.330	–	–	–	–
Date	–0.001 (0.04)	0.001	1	0.975	–0.01 (0.03)	0.05	1	0.827
Plot sex ratio treatment \times sex	0.08 (0.31)	0.06	1	0.803	–0.18 (0.32)	0.32	1	0.572
Relative experimental brood sex ratio \times sex	0.02 (1.17)	0.0004	1	0.984	–2.00 (1.16)	2.95	1	0.086
Original plot sex ratio \times sex	3.84 (3.16)	1.48	1	0.224	0.27 (3.23)	0.01	1	0.933
Relative original brood sex ratio \times sex	0.48 (1.14)	0.18	1	0.674	1.39 (1.13)	1.52	1	0.218

Summaries are derived from the multivariate normal response mixed modelling procedure in MLwiN with plot, brood and nestling as random effects. All non-significant variables were tested separately again in the final model. Provisioning rate showed significant variation between nestlings ($\chi^2_1 = 86.52$, $p < 0.001$) and broods ($\chi^2_1 = 5.51$, $p = 0.019$) but none between plots. Prey size showed significant variation between nestlings ($\chi^2_1 = 86.56$, $p < 0.001$) and broods ($\chi^2_1 = 4.25$, $p = 0.039$) and no variation between plots. The covariance between prey size and feeding rate was significant on brood level ($\chi^2_1 = 4.33$, $p = 0.037$) but not on nestling level ($\chi^2_1 = 1.27$, $p = 0.259$), $N = 194$.

6.39 ± 0.34 , female young 6.39 ± 0.29). We found no correlation between the amount of food received per hour and brood size ($\beta \pm \text{SE} = -0.19 \pm 0.24$, $\chi^2_1 = 0.65$, $p = 0.421$) or relative original brood sex ratio ($\beta \pm \text{SE} = -4.20 \pm 2.32$, $\chi^2_1 = 3.28$, $p = 0.070$) and no effect of the plot sex ratio treatment ($\beta \pm \text{SE} = 0.47 \pm 0.68$, $\chi^2_1 = 0.47$, $p = 0.493$) or the relative experimental brood sex ratio ($\beta \pm \text{SE} = 2.20 \pm 2.70$, $\chi^2_1 = 0.67$, $p = 0.414$). The total amount of food was not sex-specifically related to the original plot sex ratio ($\beta \pm \text{SE} = 9.96 \pm 8.86$, $\chi^2_1 = 1.26$, $p = 0.261$), the relative original brood sex ratio ($\beta \pm \text{SE} = 3.18 \pm 3.24$, $\chi^2_1 = 0.96$, $p = 0.326$), the plot sex ratio treatment ($\beta \pm \text{SE} = 0.001 \pm 0.88$, $\chi^2_1 < 0.001$, $p = 1.00$) or the relative experimental brood sex ratio ($\beta \pm \text{SE} = -1.84 \pm 3.30$, $\chi^2_1 = 0.31$, $p = 0.578$).

The relative male provisioning to an individual nestling was not significantly related to any of the variables tested (Table 4). Additionally, the relative male provisioning did not change with regard to nestling sex, nor were there sex-specific effects of the plot sex ratio treatment or the relative experimental brood sex ratio (Table 4).

Discussion

We found that parents fed experimentally male biased broods on average larger prey sizes with a tendency to do fewer provisioning visits. Consequently, the overall amount of food delivered did not vary between the different experimental brood sex ratios. We also found that broods in plots that were originally more male biased received more provisioning visits, larger prey and, thus, a higher amount of food, even after manipulation. Parents did not treat the two offspring sexes within the nest differently, neither in provisioning rate nor in average prey size. Furthermore, parents varied neither prey size nor provisioning rate to the individual nestling sexes in relation to the brood sex ratio treatment. Fathers and mothers also did not adjust their share of provisioning in relation to offspring sex or brood sex ratio.

Number versus size of prey items

Our data showed that broods with relatively high provisioning rates also had larger average prey sizes delivered. This is surprising given the trade-off between provisioning rate and prey size shown in earlier studies (Kluyver, 1950; Royama, 1966; Van Balen, 1973; Tinbergen, 1981). Differences in

Table 4. Model summaries examining relative male provisioning to great tit nestlings in relation to plot sex ratio treatment, relative experimental brood sex ratio (deviance of experimental brood to plot sex ratio), original plot and relative original brood sex ratio (deviance of original brood to plot sex ratio), brood size (day 10) and laying date (date).

Explanatory variable	β (SE)	χ^2	df	<i>p</i>
Final model				
Intercept	0.15 (0.12)	1.65	1	0.199
Rejected terms				
Sex	0.08 (0.16)	0.23	1	0.632
Plot sex ratio treatment	0.11 (0.25)	0.21	1	0.649
Relative experimental brood sex ratio	0.31 (0.95)	0.11	1	0.743
Original plot sex ratio	-2.00 (2.59)	0.60	1	0.438
Relative original brood sex ratio	-0.37 (0.66)	0.32	1	0.573
Brood size	-0.06 (0.08)	0.51	1	0.477
Date	-0.06 (0.04)	2.19	1	0.139
Sex \times plot sex ratio treatment	0.01 (0.35)	0.002	1	0.966
Sex \times relative experimental brood sex ratio	0.65 (1.26)	0.26	1	0.608
Sex \times original plot sex ratio	-0.18 (3.88)	0.002	1	0.964
Sex \times relative original brood sex ratio	0.82 (0.92)	0.79	1	0.372

Summaries derived from the binominal response modelling procedure in MLwiN where all non-significant effects were tested separately again in the final model. Plot, brood and nestling were kept as random effects in the model with significant variation between broods ($\chi^2_1 = 4.94$, $p = 0.026$), $N = 193$.

parental or territory quality can result in the positive correlation between provisioning rate and prey size such that parents of high body weight (Lifjeld, 1988) or birds in a good habitat (Naef-Daenzer et al., 2000) bring more often food of larger size to the brood. If habitat quality alone would cause such a positive correlation, we would also expect a positive correlation between the feeding traits of male and female partners. In our data, this was only the case for provisioning rate to individual nestlings but not to entire broods.

Average prey size delivered and to some extent also provisioning rate were positively correlated with brood size as was the 'total amount of food'. In larger broods individual nestlings received food at similar rates as in smaller broods but were fed, on average, larger prey items. This contradicts results of other studies, which found that the provisioning rate did not increase proportionally with the number of young in the nest (Royama, 1966; Rytönen

et al., 1996; Tinbergen & Verhulst, 2000; Stoeckl et al., 2001). Our results indicate that parents adjusted brood size to the food availability in their territory and/or that they adjusted prey size and provisioning rates to the current brood needs.

Why did male nestlings not get more food than their female siblings?

Male great tit nestlings are significantly larger than female nestlings at day 14 (5% heavier, own observation) and have been shown to out-compete their sibling sisters under intensified competition (Oddie, 2000; Nicolaus et al., 2009). Interestingly, we did not find that male young received more food than female young, despite being heavier and female young were not fed differently in male or female biased broods. Apparently, food needs to be restricted or competition intensified for that females are out-competed by their male nest mates (Oddie, 2000; Nicolaus et al., 2009). That parents provision the two offspring sexes within a brood equally despite sexual size dimorphism, has also been described in earlier studies (Whittingham et al., 2003; Boncoraglio et al., 2008). There are four possible explanations for this finding: (1) The sexes allocate the same amount of resources into different body functions especially when resources are limited (Tschirren et al., 2003; Nicolaus et al., 2009). Nicolaus et al. (2009) showed in a study on the same population that under 'stressful' nutritional conditions males seem to invest relatively more in weight while females invest more in wing length. (2) Stamps (1990) proposed that sex-biased provisioning in relation to sex differences in energy requirements should mainly occur in species with strong size dimorphism. Indeed, higher food consumption rates of the larger sex have only been shown in species with strong sexual size dimorphism (Teather, 1987; Yasukawa et al., 1990; Magrath et al., 2007). Studies on species with smaller size dimorphism (like the great tit) mostly failed to find differences between the offspring sexes in the quality or quantity of food received (Howe, 1979; Leonard et al., 1994; Whittingham et al., 2003). In those species, differential provisioning in relation to offspring sex might only be expected if the sexes have different effects on their parent's reproductive success after independence (Stamps, 1990). (3) Parents may lack cues that allow discrimination of the offspring sexes. Although great tit nestlings show significant sexual size dimorphism at day 14, differences at the time of the video observation were still smaller (non-significant 4% weight difference at day 6). In some species

parents could use differences in feather coloration for discrimination of offspring sexes where there is no apparent size difference (Gowaty & Droge, 1991). In other species the two sexes differ in begging behaviour (Teather, 1992; Saino et al., 2003) and parents reacted to this difference by adjusting their provisioning behaviour (Teather, 1992; Boncoraglio et al., 2008). However, whether mechanisms for nestling sex recognition also exist in great tits is not known. (4) Parents need to trade-off the time needed for discrimination of offspring sexes with foraging time, and the benefits of discrimination may be outweighed by the resulting lower foraging yield. Stamps et al. (1985) found in budgerigars (*Melopsittacus undulatus*) that fathers reacted to offspring sex ratio but not individual offspring sex which indicates a trade-off between parental provisioning rate and choosing among potential food recipients.

The effect of sex ratio on parental provisioning

We only found an effect of sex ratio on prey size when looking at within plot effects of the manipulation. There was no indication that prey size and provisioning rate to broods were affected by the overall plot sex ratio treatment. A likely explanation for this is that plots differed a lot in prey availability (indicated by the relation between original plot sex ratio and provisioning behaviour). Then we simply might have lacked the power to detect an overall plot treatment effect.

Parents reacted to the brood sex ratio manipulation by adjusting the size of prey items brought to the brood. However, this did not result in differences in the total amount of food provided to experimentally sex ratio biased broods, probably, because simultaneously the provisioning rate was slightly altered. This indicates a trade-off between parental provisioning rate and prey size which could happen if higher prey selectivity causes the provisioning rate to drop or vice versa (Lifjeld, 1988; Grieco, 2002). Based on this, our finding that parents provided larger prey items to male biased broods could have the following explanations: (1) Male and female nestlings differ in their specific nutritional need or metabolic properties. Parents could then alter their provisioning strategy to the entire brood, not paying the cost of nestling sex discrimination. Energetic value of prey items might not linearly increase with size as was suggested by a study on house sparrows (*Passer domesticus*) where only delivery of the largest food items was positively related to fledgling mass and recruitment (Schwagmeyer & Mock, 2008). Thus, delivery of

larger prey items at slightly lower rates might indicate higher quality prey delivered to male biased broods. (2) Food solicitation activities of offspring might be more costly in male biased broods because of higher competitive interactions, or because larger males might loose more energy during food solicitation activities. Then delivery of larger prey items at lower rates could be an adaptive response to decrease the number of visits and thereby the energetically costly activities. (3) If male nestlings indeed have higher begging activities, parents might also reduce feeding rates and bring larger prey items to reduce the risk of predation. These explanations do not require individual offspring sex recognition, but could work if parents respond directly to brood solicitation rates.

We found a correlation between parental provisioning behaviour and the original plot and relative original brood sex ratio. Most likely parental provisioning behaviour depended on factors that co-varied with original sex ratio and that also affected provisioning behaviour like plot and/or territory quality or parental traits. These relations are potentially very important because they can indicate why sex ratios vary in the first place.

In conclusion, our study showed that parents did not treat the two offspring sexes differently which is in agreement with other studies (Newton, 1978; Howe, 1979; Leonard et al., 1994; Whittingham et al., 2003). Nevertheless, in our study parents did change the prey size delivered in relation to the brood sex ratio manipulation. Bringing larger prey to male biased broods might decrease intra-brood competition, reduce predation risk or potentially increase the quality of prey delivered. We, therefore, strongly emphasize the importance of incorporating more aspects than solely provisioning rates when investigating parental provisioning behaviour especially because opposing effects of the different provisioning traits might level each other out.

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